

RESEARCH ARTICLE

Alexander S. Aruin · Mark L. Latash

The role of motor action in anticipatory postural adjustments studied with self-induced and externally triggered perturbations

Received: 9 March 1995 / Accepted: 5 June 1995

Abstract This study investigated the relation between the magnitude of a motor action triggering a postural perturbation and the magnitude of anticipatory postural adjustments. Subjects stood on a force platform and held, in extended arms, a balloon with a 2.2-kg load suspended on a rigid cord. In different series, unloadings were induced by fast bilateral shoulder abduction movements, by popping the balloon with a tack taped to the subject's right middle finger, or by the experimenter popping the balloon. Anticipatory postural adjustments were seen during all self-initiated unloadings as changes in the level of activation of postural muscles and in displacements of the center of pressure. However, absolute values of these changes were significantly smaller in the series with balloon popping as compared to the series with shoulder abductions. Such reactions were absent when the unloading was triggered by the experimenter. We conclude that a self-triggered perturbation is always associated with anticipatory postural adjustments, while the magnitude of the adjustments may be scaled with respect to the magnitude of a motor action used to induce the perturbation.

Key words Posture · Anticipatory adjustment · Voluntary movement · Electromyogram · Human

Introduction

When a task to perform a fast, focal voluntary movement coexists with a task to maintain equilibrium in the field

of gravity or posture of a limb, feedforward adjustments in the activity of apparently postural muscles are used to counteract the expected perturbing forces. These reactions are generated by the central nervous system in anticipation of a perturbation, and, therefore, they have been termed "anticipatory postural adjustments" (for a review see Massion 1992). Anticipatory adjustments have been studied in a variety of experimental procedures, including voluntary foot movements (Alekseev et al. 1979; Dietz et al. 1980), trunk movements (Oddsson and Thorstensson 1986), and arm movements in standing subjects (Belenkiy et al. 1967; Bouisset and Zattara 1981; Cordo and Nashner 1982; Friedli et al. 1984, 1988; Riach et al. 1992; Aruin and Latash 1995), as well as in tasks restricted to upper extremities that did not involve maintenance of the vertical posture (Dufosse et al. 1985; Struppler et al. 1994).

Voluntary arm movements by standing subjects have been most frequently used to study anticipatory postural adjustments. This approach, however, has its pitfalls. In particular, slow movements do not usually involve anticipatory postural adjustments (Horak et al. 1984, Crenna et al. 1987). Thus, differences in anticipatory postural adjustments in different subjects may reflect both differences in their central mechanisms of anticipatory postural control and the ability to move fast (cf. Bazalgette et al. 1986; Dick et al. 1986; Viallet et al. 1987; Latash et al. 1995b).

Several studies used nongraded postural perturbations triggered by a voluntary movement. These experiments involved a postural task performed by one arm and an action by the other arm that could bring about a postural perturbation (Dufosse et al. 1985; Paulignan et al. 1989; Struppler et al. 1993). In particular, these studies raised a basic question related to the relative importance of predictability of a perturbation and a major motor action used to trigger the perturbation. Struppler et al. (1994) demonstrated that a predictable perturbation induced by an experimenter did not give rise to anticipatory postural adjustments, while the same perturbation induced by the subject did. Dufosse et al. (1985) reported that unloading

A. S. Aruin
Department of Physical Medicine and Rehabilitation,
Rush-Presbyterian St. Luke's Medical Center,
Chicago, IL 60612, USA

M. L. Latash (✉)
Biomechanics Laboratory,
Department of Exercise and Sport Science,
Pennsylvania State University,
University Park, PA 16802, USA;
Fax: +1-814-865-2440

of an arm triggered by a finger movement of the other arm failed to induce anticipatory postural adjustments, while the same unloading triggered by a movement of the other arm involving proximal muscle groups induced anticipatory adjustments. A preliminary conclusion from these studies was that predictability of a perturbation was not sufficient for generation of anticipatory postural adjustments, and a major action involving large (proximal) muscle groups was required.

We have recently designed a method for investigation of anticipatory postural adjustments in standing subjects that involves dropping loads from extended arms (Aruin et al. 1994; Latash et al. 1995b). Such unloadings were triggered by a thumb movement of the right arm. The induced postural perturbations were apparently predictable and independent of the ability of the subject to perform fast voluntary movements. Our observations have shown that dropping loads is associated with anticipatory postural adjustments seen, in particular, as changes in the background electrical activity of the trunk and leg muscles as well as in the displacements of the center of pressure. These changes were, however, smaller than those seen during fast arm movements. The question of whether thumb movement is a "minor action" or a "major action" is debatable. So, we have decided to use the smallest possible finger movement to trigger postural perturbations in standing subjects, to quantify anticipatory changes in the muscle activity and displacements of the center of pressure, and to answer the basic question: *Is self-triggered perturbation in a standing subject always accompanied by anticipatory postural adjustments?*

Materials and methods

Subjects

Seven healthy male subjects, mean age 38.4 years (± 3.0 SE), mean weight 75.7 kg (± 3.03 SE), and mean height 1.746 m (± 0.038 SE), without any known neurological or motor disorders, took part in the experiment. The subjects gave informed consent according to the procedure approved by the Human Investigation Committee of the Medical Center.

Apparatus

The subjects stood on a force platform AMTI OR-6 (Fig. 1). The signals from the platform were amplified and used to measure reaction forces in three orthogonal directions (along the direction of gravity F_z , parallel to the ground in a sagittal plane F_x , and parallel to the ground in a frontal plane F_y) and moments of forces in two directions (in a sagittal plane, M_y , and in a frontal plane, M_x). A 2.2-kg load was either directly held by the subject in his arms or suspended on a short, rigid cord from an inflated balloon that was held by the subject. The diameter of the balloon was 0.3 m. The load was solid and brick-shaped, with a longest dimension of 0.3 m. In some series, a tack was taped to the middle finger of the subject's right hand.

Three two-axis goniometers (Penny and Giles) were taped on body segments and measured angles in a sagittal plane in the ankle, knee, and hip joints. Acceleration was measured by a miniature unidirectional accelerometer (Sensotec). The accelerometer was taped to the left palm just below the middle finger. Its signals were used only for trial alignment. Disposable pediatric electro-

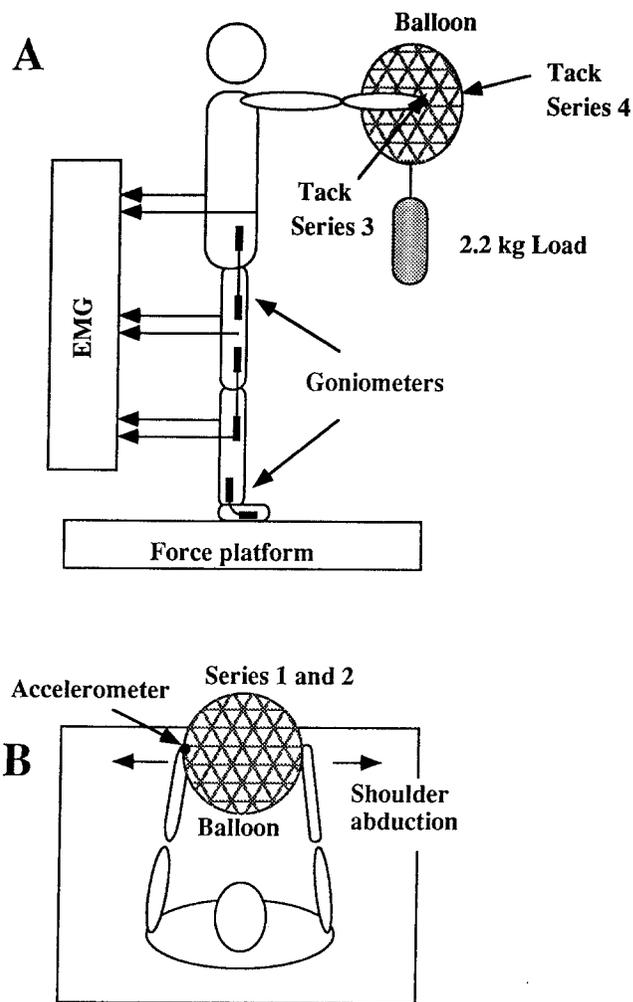


Fig. 1A, B The experimental setup. **A** Lateral view of the subject. Note that, in series 3, a tack was taped to the subject's right middle finger; in series 4, the tack was taped to the experimenter's right index finger and was not seen by the subject; in a pilot series, the tack was taped to the experimenter's right index finger and was seen by the subject. **B** View of the subject from above. *Arrows* show the direction of shoulder movements

cardiographic electrodes were used to record the surface electromyographic (EMG) activity of the following muscles: rectus abdominis, erector spinae, rectus femoris, biceps femoris, soleus, and tibialis anterior. The electrodes were placed over the muscle bellies. The distance between two electrodes of a pair was about 4 cm. Signals from the electrodes were amplified ($\times 3000$) and band-pass filtered (60–500 Hz). Later, these signals were rectified and low-pass filtered at 100 Hz. All the signals were sampled at 500 Hz with a 12-bit resolution. A Mac-IIci computer with a customized software based on the LabView-2 package was used to control the experiment, collect the data, and perform most of the analyses.

Procedure

The procedure involved four experimental series, each series consisting of six trials. Time intervals between the trials within a series were 8 s. Intervals between the series were about 1 min. Fatigue was never an issue. Prior to the first and the second series, the subjects were given two practice trials. There were no practice trials prior to the third and the fourth series. Two more pilot series were performed.

During the first series, the subject held the 2.2-kg load between his hands in extended arms. The palms pressed on the load surface and faced each other; the fingers were extended. The subject was looking straight at the load. At the computer-generated tone signal, the subject was required to release the load by a low-amplitude, fast abduction movement of both shoulders. The subject was told that he had up to 3 s to perform the task in a self-paced manner. The load was caught by the experimenter.

The second series was similar to the first one, but the subject held, in a similar fashion, an inflated balloon with the same load suspended on a short cord. The diameter of the loaded balloon was approximately the same as the size of the load. At the tone signal, the subject was required to release the balloon by a quick abduction of both shoulders.

During the third series, the initial position of the subject, the balloon, and the load were the same as in the second series. At the tone signal, the subject was required to pop the balloon with a light touch of the tack attached to the middle finger of the right hand.

The fourth series of experiments was similar to the third one, but the balloons were popped by the experimenter at unpredictable intervals after the computer-generated tone signal. We preserved the tone signal in this series to make the conditions comparable across the series. The eyes of the subject were closed in this series.

Two pilot series were run on two subjects. In the first pilot series, the subject was asked to stand in the same position as in all the previously described series, but without a load between the hands. At the tone signal, the subject was asked to make a fast, bilateral shoulder abduction movement similar to those used for unloading in series 1 and 2. During the second pilot series, the subject held an inflated balloon with the load suspended on a rigid cord. The balloon was popped by the experimenter after the tone signal. The experimenter's finger with the tack touched the balloon from above, so that the subject could see it at any time. The subject was instructed to watch the finger of the experimenter as it approached the balloon.

Data processing

The trials were viewed off-line on a monitor screen and aligned according to the first visible deflection of the acceleration signal from the accelerometer taped to the left palm. We shall refer to this time as "time zero" (t_0). For further analyses, all the trials of a series by a subject were averaged. The following integral EMG measures were used: (1) J_1 : anticipatory activity – an integral from -100 to $+50$ ms with respect to t_0 ; (2) J_2 : background activity – an integral from -500 to -350 ms with respect to t_0 . We feel confident in referring to EMG changes in the time interval from -100 to $+50$ ms as "anticipatory," because this interval of integration did not allow any feedback-based changes in the muscle activity (cf. Aruin and Latash 1995). The ratio $\Delta J = (J_1 - J_2) / J_2$ was used to characterize the anticipatory changes in the activity of the postural muscles. Horizontal displacements of the center of pressure in the anterior-posterior (ΔCP) direction were calculated using the following approximation: $\Delta CP = M_y / F_z$.

Statistical methods included versions of the Student's t -test and nonparametric statistics.

Results

Figure 2 shows the kinematic and EMG patterns in one of the subjects in the first series. In this series, the subject held a 2.2-kg load in extended arms and released it with a fast, bilateral shoulder abduction movement. Six trials were averaged after being aligned according to the first visible deflection (t_0) of the signal from an accelerometer taped to the left palm. Note that holding the load required the subject to activate postural muscles at the

dorsal parts of the trunk and of the legs. A typical pattern of the changes in the muscle activity prior to the unloading involved an anticipatory inhibition of the EMG activity of erector spinae, biceps femoris, and soleus starting from about 100 ms prior to t_0 . There was also a small anticipatory increase of the EMG activity in rectus abdominis, rectus femoris, and tibialis anterior, as well as small displacements of the hip and knee joints. Note that the anticipatory changes in the activity of postural muscles were accompanied by a shift of the center of pressure.

The second series involved dropping the load suspended from a balloon with a similar bilateral shoulder abduction. It was accompanied by similar anticipatory changes in the EMGs and the center of pressure to the first series. In a pilot series, two subjects performed similar shoulder abduction movements without any load. These movements, by themselves, did not induce any visible anticipatory changes in any of the recorded signals (EMGs and displacements of the center of pressure are shown in Fig. 3). Note that peak acceleration values in Figs. 2 and 3 are similar.

During the third series of experiments, the subject popped the balloon with the tack taped to the right middle finger. Figure 4 shows a representative set of data for one of the subjects. There are small anticipatory displacements of the hip and knee angles and a small displacement of the center of pressure. However, the activity of erector spinae, biceps femoris, and soleus does not show as clear signs of anticipatory inhibitions, as in Fig. 2. The only apparent anticipatory EMG event is the early burst of activity in rectus abdominis (RA in Fig. 4). Note, also, much larger deviations in all the joints and forces and in the center of pressure that occur at times between 100 and 200 ms after the time of alignment.

Popping the balloon by the experimenter (series 4) did not lead to any anticipatory events in any of the kinematic, dynamic, or EMG records (Fig. 5). The first bursts of activity are seen in rectus abdominis, rectus femoris and tibialis anterior at a latency of about 60 ms after the balloon explosion. Similar patterns were observed in the series when the subjects closed the eyes (illustrated in Fig. 5) and in the pilot series when the subject could see, and, moreover, was specifically instructed to watch how the experimenter touched the top of the balloon with the tack (Fig. 6).

Displacements of the center of pressure in the anterior-posterior direction demonstrated apparent anticipatory components in the first three series that involved self-triggered unloading. Figure 7A shows the displacements of the center of pressure (ΔCP) for one of the subjects in all four series, while Fig. 7B presents absolute values of ΔCP measured at the time of alignment (zero in Fig. 7A) with respect to center of pressure position 0.4 s earlier (-0.4 s in Fig. 7A) and averaged across the subjects. Note that the values of ΔCP during the first and the second series were not significantly different from each other ($P > 0.1$; two-group, paired, two-tailed Student's t -test) and were both significantly different from zero ($P < 0.05$;

Fig. 2 Kinematic and EMG patterns (means of six trials) in a subject dropping a 2.2-kg load with a fast, bilateral shoulder abduction movement (series 1). Note an anticipatory backward displacement of the center of pressure (ΔCP in the lower left panel), a small, anticipatory activation of rectus abdominis (RA), rectus femoris (RF), and tibialis anterior (TA), and an anticipatory inhibition of erector spinae (ES), biceps femoris (BF), and soleus (SOL). EMGs of erector spinae, biceps femoris, and soleus are inverted for better visualization; EMG scales are in arbitrary units. Individual trials were aligned based on the signal from an accelerometer (*Accel*) taped to the left palm (*arrows* show the time of alignment; *F_x*, *F_y* horizontal components of reaction forces)

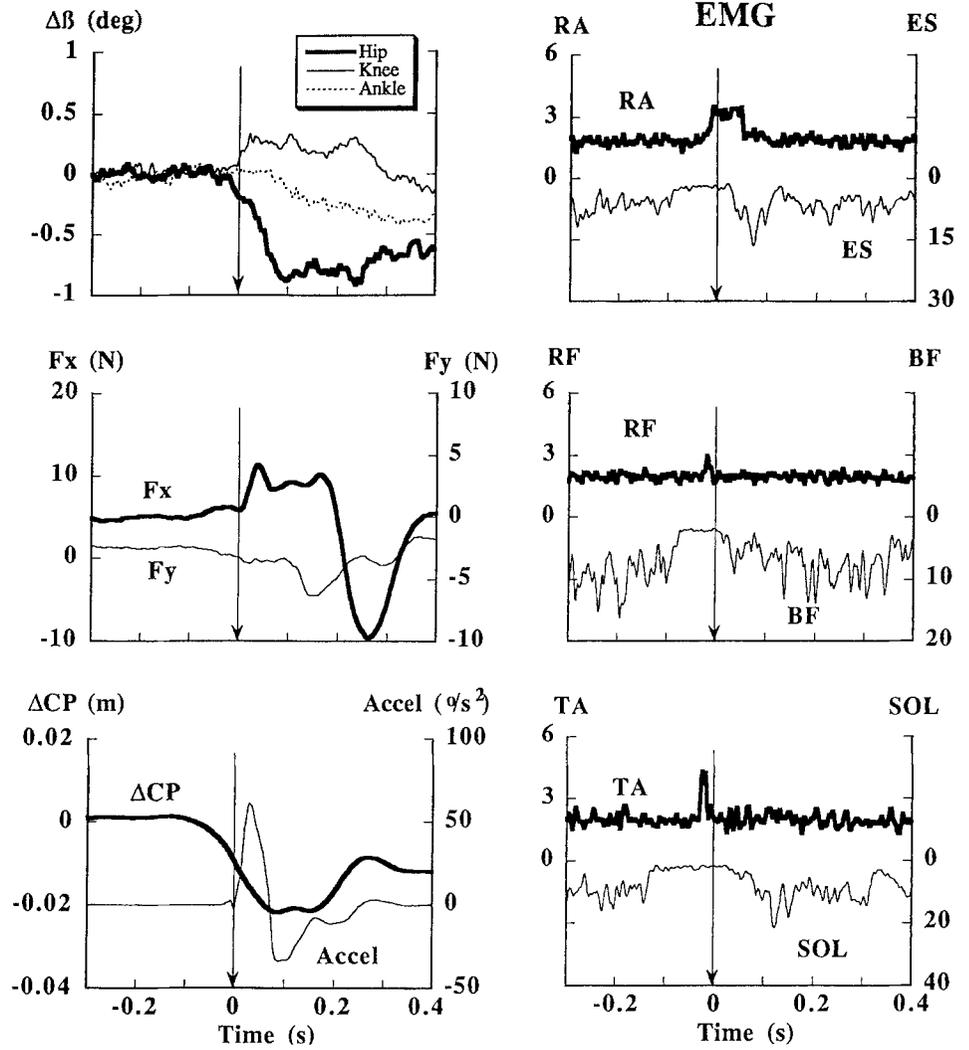


Fig. 3 Kinematic and EMG patterns (means of six trials) in a subject during a fast, bilateral shoulder abduction movement (a pilot series). Note the lack of anticipatory changes in the EMGs as well as in the position of the center of pressure. Individual trials were aligned based on the signal from an accelerometer (*Accel*) taped to the left palm (*arrows* show the time of alignment). EMG scales are in arbitrary units

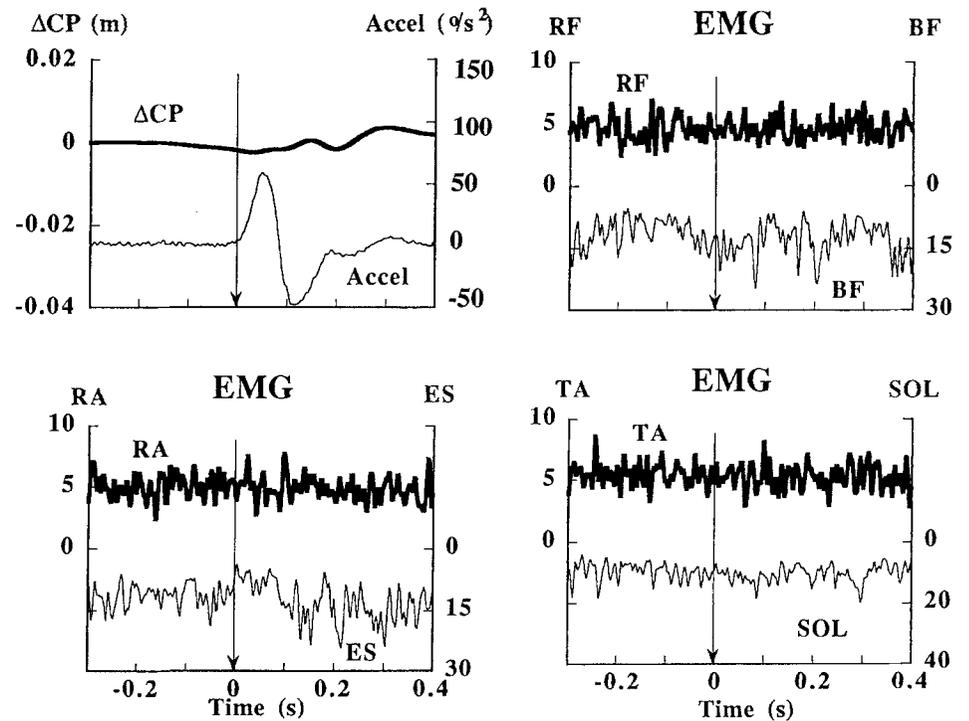
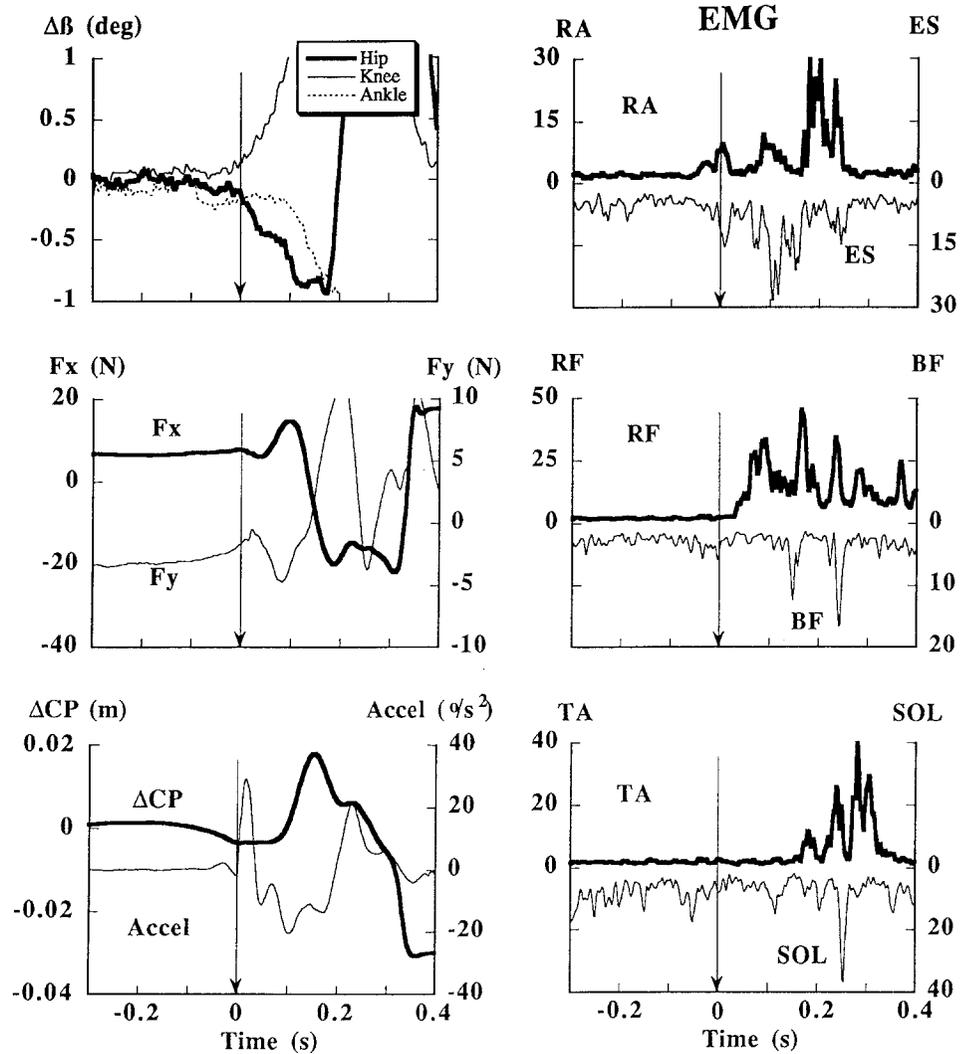


Fig. 4 Kinematic and EMG patterns (means of six trials in one subject) for a series of trials with self-inflicted unloadings triggered by popping the balloon (with the 2.2-kg load attached). Note the smaller anticipatory displacement of the center of pressure (ΔCP) as compared to Fig. 2. The only apparent anticipatory EMG event is an EMG burst in rectus abdominis (RA). Note also larger deviations of the leg joints, center of pressure, and reaction forces that start at about 100 ms after the time of alignment (shown by arrows). Scales and abbreviations are the same as in Fig. 2



single-group, two-tailed Student's *t*-test). During the third series with self-triggered unloadings, mean ΔCP was smaller than in either of the first two series ($P < 0.05$; two-group, paired, two-tailed Student's *t*-test) and was significantly different from zero ($P < 0.05$; single-group, two-tailed Student's *t*-test). Averaged value of ΔCP during unexpected unloadings (the fourth series) was significantly smaller than in any of the first three series ($P < 0.05$; two-group, paired, two-tailed Student's *t*-test) and was not different from zero ($P > 0.1$; single-group, two-tailed Student's *t*-test).

Anticipatory changes in the EMGs were quantified with the help of a ratio $\Delta J = (J_1 - J_2) / J_2$, where J_1 is EMG integral from -100 to $+50$ ms with respect to the time of alignment (t_0), and J_2 is EMG integral from -500 to -350 ms (see Materials and methods). For each muscle and for each series, the values of ΔJ were averaged across the subjects. The averaged values with standard error bars are presented in Fig. 8. There was statistically significant inhibition of the background activity of erector spinae in the second series ($t = -4.344$, $P < 0.05$, single-group Student's *t*-test), of biceps femoris in the second and third series ($t = -3.84$, $P < 0.05$ and $t = -3.49$, $P < 0.05$,

correspondingly), and of soleus in the first three series ($t = -4.7$, $P < 0.01$ for the first series; $t = -6.16$, $P < 0.005$ for the second series; and $t = -5.0$, $P < 0.01$ for the third series), but not in the fourth series, with unexpected unloading (for each muscle, $P > 0.1$). The magnitude of this effect in erector spinae and biceps femoris was significantly larger in the second series (dropping the balloon with the load) than in the third series (popping the balloon). For erector spinae, $t = 6.48$, $P < 0.005$; for biceps femoris, $t = 3.23$, $P < 0.05$ (two-tailed, paired Student's *t*-test). Rectus abdominis, rectus femoris, and soleus tended to demonstrate an anticipatory increase in the background activity, but these effects were not significant statistically.

Discussion

Anticipatory postural adjustments were observed in all our experiments with self-initiated unloadings. These adjustments were seen, in particular, when the unloadings were triggered by a slight movement of a finger popping the balloon and releasing the load. They were not seen in

Fig. 5 Kinematic and EMG patterns (means of six trials in one subject) for a series of trials with unexpected unloadings induced by popping the balloon with the load by the experimenter. The subject stood with his eyes closed. Note the lack of anticipatory reactions in any of the traces. Scales and abbreviations are the same as in Fig. 2

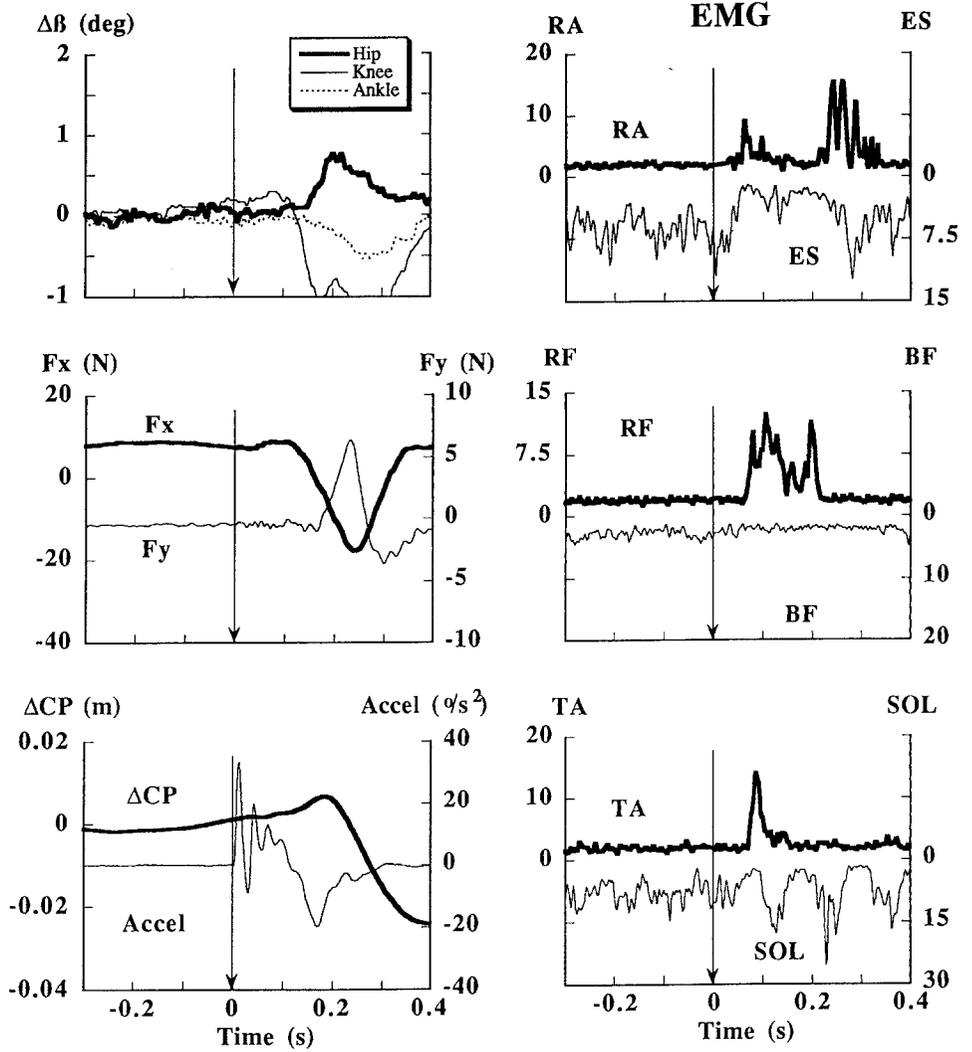
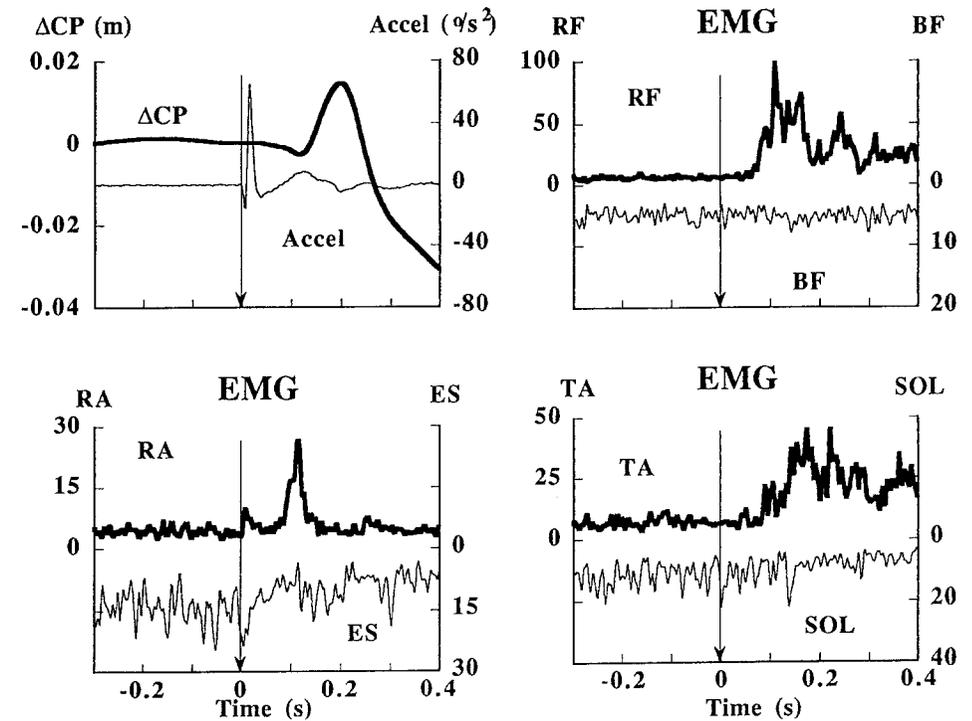


Fig. 6 Kinematic and EMG patterns (means of six trials in one subject) for a pilot series of trials with unloadings induced by popping the balloon with the load by the experimenter while the subject was watching how the experimenter popped the balloon. Note the lack of anticipatory reactions and large later responses. Scales and abbreviations are the same as in Fig. 2



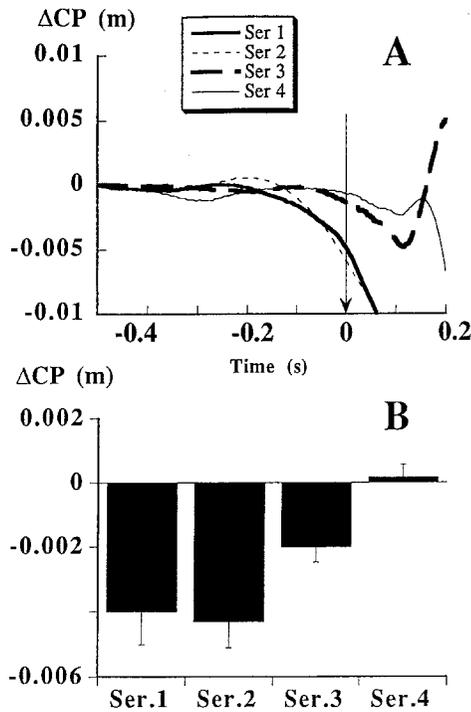


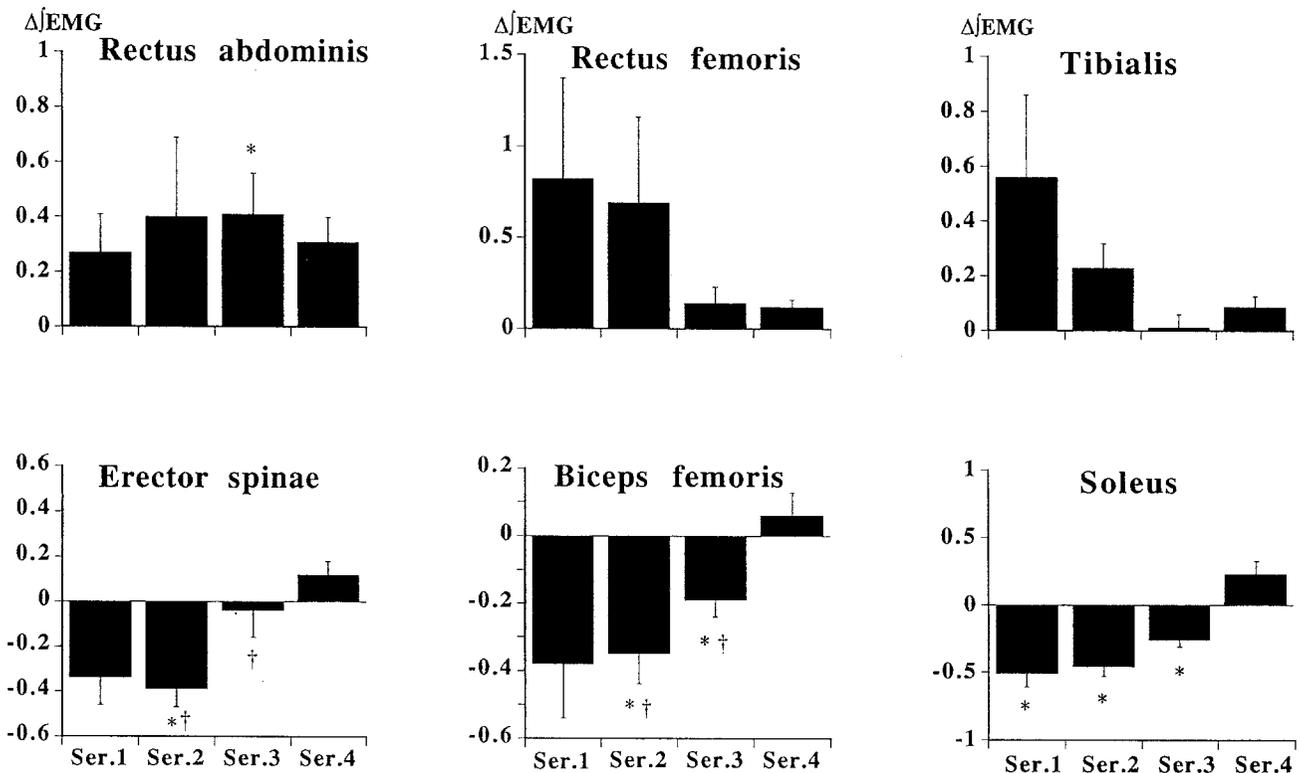
Fig. 7 **A** Displacement of the center of pressure (Δ CP) in the anterior-posterior direction for one of the subjects in four series; each record is the mean of six trials. Note anticipatory changes in the first two series and the lack of them during unexpected unloadings. **B** Mean Δ CP values for different series (Ser 1 to Ser 4) averaged across seven subjects (with SE bars). The displacement was measured at the time of alignment with respect to its value 400 ms prior to this time

the experiments when the balloon was popped by the experimenter. These findings let us formulate the following two major hypotheses related to the generation of anticipatory postural adjustments: (1) self-initiation of a postural perturbation by a motor action is sufficient for the generation of an anticipatory postural reaction; and (2) the magnitude of an anticipatory postural adjustment is, to a large extent, determined by the magnitude of the voluntary focal action used to bring about the perturbation. Let us discuss these hypotheses and their consequences in more detail.

The first hypothesis

This hypothesis seems contradictory to the conclusions drawn by Dufosse et al. (1985; see also Paulignan et al. 1989), who did not observe anticipatory postural adjustments in an arm performing a postural task when it was unloaded by pressing a trigger with a contralateral finger. Such reactions were seen when a similar unloading was triggered by a major movement of the contralateral arm involving proximal muscles. However, the difference might have resulted from relatively small anticipatory adjustments in the experiments by Dufosse and his colleagues that did not reach a level of statistical signifi-

Fig. 8 Averaged across the subjects, values of the relative changes in the background EMG activity (Δ EMG) are shown with standard error bars. *Statistically significant changes in the background EMG ($P < 0.05$ according to single-group, two-tailed Student's *t*-test). †Statistically significant difference in Δ between two experimental series ($P < 0.05$ according to the paired, two-tailed Student's *t*-test)



cance, i.e., from a quantitative rather than a qualitative difference. Note that anticipatory postural adjustments in our experiments during perturbations triggered by finger movements were significantly smaller than during similar perturbations induced by shoulder movements.

The findings by Struppler et al. (1993) have suggested that predictability, by itself, is insufficient for anticipatory postural adjustments if a postural perturbation is induced by an experimenter without any motor action by the subject, even if the perturbation is timed to a metronome. However, if the subject performed a focal movement that was physically unrelated to the perturbation but synchronized with an action by the experimenter inducing the perturbation, anticipatory postural adjustments did occur. These findings are in a good correspondence with the results of our present study, particularly with our pilot observations, where watching the experimenter popping the balloon did not bring about anticipatory postural adjustments. They suggest that a motor action by the subject is a *necessary condition* for anticipatory postural adjustments; it is a *sufficient condition*, as well, according to our first hypothesis. However, in a previous study of catching loads by standing subjects, we described adjustments in the activity of proximal arm muscles (deltoids) that happened prior to the load contact, i.e., in conditions of a *predictable perturbation that was not triggered by a subject's action* (Aruin et al. 1994; Latash et al. 1995b). Such adjustments were typically not seen, however, in leg or trunk muscles. These findings are somewhat similar to the data described by Lacquaniti and Maioli (1989) in their study of catching.

Let us suggest that the seeming contradiction between the adjustments in the muscle activity prior to catching and the conclusion by Struppler and his colleagues may, in fact, originate from the loosely defined notions of "focal movement" and "postural adjustment." We suggest use of the term "anticipatory postural adjustment" for changes in the background activity of a muscle that are: (a) timed with respect to a focal movement; (b) cannot be attributed to feedback mechanisms; and (c) may be independent of the physical properties of the focal movement. The last condition seems to us rather important. It is based on an accepted view that the functional role of anticipatory postural adjustments is to attenuate the perturbing effects on posture or body equilibrium of a planned action (Bouisset and Zattara 1990; Massion 1992). This condition implies that anticipatory postural reactions should be scaled with respect to an anticipated consequence of a focal action rather than to the action itself.

In our experiments, voluntary movements by the subjects (focal actions) did not involve, by themselves, any significant perturbation in the anterior-posterior direction. This is obvious for finger movements and was confirmed, for shoulder movements, by the pilot observations of the lack of visible displacements of the center of pressure when the same movements did not induce the unloading (Fig. 3). Therefore, postural adjustments were apparently related to the predictable consequences of the

shoulder or finger movements, i.e., to the task context, but not to the focal movements themselves. During catching tasks, preparation for catching may be considered a separate motor action similar to preparation for landing (Melvill-Jones and Watt 1971a,b) or to any other contact with an external object, since no other focal action takes place. As such, its mechanisms may differ from those involved in anticipatory postural adjustments.

The second hypothesis

The second hypothesis looks somewhat counter-intuitive and contradictory to what has just been said in the previous section. The system seems to function in a suboptimal fashion by grading anticipatory postural adjustments based on the magnitude of a focal motor action that is used to trigger a perturbation while the magnitude of the perturbation remains unchanged. As it has been mentioned, the function of anticipatory postural adjustments is to counteract an expected perturbation. Since, in our experiments, the magnitude of the perturbation was always the same and, therefore, totally predictable, it would be natural for postural adjustments to correlate with the magnitude of the perturbation, i.e., to stay constant, rather than to change with motor action that is only contextually but not quantitatively tied to the perturbation.

Note that there were larger displacements of the center of pressure and of the major leg joints in the experiments with popping the balloon, as compared to experiments with load dropping, that started about 100 ms after the perturbation (cf. Figs. 2, 3). Corrective, feedback-triggered bursts of activity in the postural muscles were seen at latencies of about 60–70 ms (cf.; Nashner and Woollacott 1979; Nashner and Cordo 1981; Allum 1983; see Figs. 2, 3). In the experiments with balloon popping, startle reactions could also be seen in the flexor muscles at longer latencies (cf. Strauss 1929; Rossignol 1975). If one takes into account typical values of the electromechanical delay, the time interval of 100 ms was unlikely to involve any significant feedback-triggered changes in the mechanical channels. So, we assume that our observations reflected the direct mechanical effects of the unloading and the effects of anticipatory postural adjustments. Since the unloading was always standard, the differences may be attributed to different efficacy of anticipatory postural adjustments. Thus, the findings of larger mechanical deviations in cases when the perturbation was triggered by touching the balloon with the tack suggest that anticipatory postural adjustments, in these trials, were indeed suboptimal.

We seem to have come to a contradiction embedded in the very notion of anticipatory postural adjustments. On the one hand, the definition of anticipatory postural adjustments (suggested in the previous section) implies their relative independence of the physical properties of the triggering movement. In particular, in our experiments, postural perturbations were apparently unrelated

to the physical characteristics of voluntary movements performed by the subjects. However, the experiments demonstrated *a dependence of the magnitude of anticipatory postural adjustments upon the physical properties of the focal movement, while postural perturbation remained the same in all the series*. All this looks very confusing and suggests that the central nervous system is not as “smart” as we used to think. In conditions of absolutely predictable and reproducible postural perturbations, it makes an unnecessary and potentially harmful adjustment in the magnitude of anticipatory postural adjustments to the magnitude of the focal movement, leading to larger deviations of the center of pressure and leg joints.

Trying to put things together

In a previous work (cf. Burleigh et al. 1994; Palmer et al. 1994; Latash et al. 1995a), we have suggested that postural adjustments may, in fact, constitute an inherent part of a motor command generated by a hypothetical controller and expressed in a higher-order variable. This view of a common controller for the focal and postural commands may be contrasted to the idea of separate controllers for these commands (Massion 1992). This hypothetical command is later transformed (processed), giving rise to commands to individual joints. The process of this transformation is assumed to reflect, in particular, prior experience of the subject with the task or with similar tasks. Classification of the joints into “focal” and “postural” may be done by the experimenters but not by the central nervous system. According to this scheme, one may expect commands to apparently postural joints to be closely tied to commands to apparently focal joints. Thus, anticipatory postural adjustments are not an addition to a “voluntary motor command” but an inherent component of this command. This scheme suggests the possibility of a close relation between the magnitude of anticipatory postural adjustments and the magnitude of a motor action that triggers a postural perturbation, if the same transformation process is used.

Our experiments involved movements which Bernstein (1947) would have probably attributed to level C of his hierarchical scheme, i.e., simple manipulations with objects in the space field. The actions, by themselves, did not endanger equilibrium. Postural perturbations resulted from a contextual interaction of the focal voluntary movements with the load. Dropping a load is apparently a rather common action and, as such, it did not present a tough task for the subject’s central nervous system (an appropriate transformation of the central command into commands to individual joints was available). In Bernstein’s terms, this action has a developed apparatus of background corrections. Popping the balloon is apparently an action that is rather uncommon. Its effects may be compared to the rebound experienced during rifle shooting. The basic feature of such phenomena is a grossly distorted relation between the magnitude

of a voluntary action and the magnitude of an ensuing perturbation. In such cases, apparently, the central nervous system does not have in stock an appropriate transformation of the central command into commands to individual joints, and scales the postural adjustments with respect to the characteristics of the voluntary movement using an available, albeit inadequate transformation. We may only speculate that prolonged practice would have probably brought about an increase in the magnitude of postural adjustments to an appropriate level, just as it happens in experienced marksmen who do not show major postural perturbation during shooting (cf. Belenkiy et al. 1967).

Acknowledgments The authors are grateful to Prof. Vladimir Zatsiorsky for many helpful discussions and to Mark Shapiro for the skillful programming assistance. This study was in part supported by grant HD30128 from the National Center for Medical Rehabilitation Research, NIH.

References

- Alekseev MA, Dobronravova IS, Naidel AV, Smetanin BN (1979) On the mechanism of postural adjustment during foot movements (in Russian). *Hum Physiol* 5: 579–588
- Allum JHJ (1983) Organization of stabilizing reflex responses in tibialis anterior muscles following ankle flexion perturbations of standing man. *Brain Res* 264: 297–301
- Aruin AS, Latash ML (1995) Directional specificity of postural muscles in feed-forward postural reactions during fast voluntary arm movements. *Exp Brain Res* 103: 323–332
- Aruin AS, Nicholas JJ, Gottlieb GL, Lee KC, Latash ML (1994) Anticipatory reactions during dropping and catching weights. *J Biomech* 27: 604
- Bazalgette D, Zattara M, Bathien N, Bouisset S, Rondot P (1986) Postural adjustments associated with rapid voluntary arm movements in patients with Parkinson’s disease. *Adv Neurol* 45: 371–374
- Belenkiy VY, Gurfinkel VS, Pal’tsev YI (1967) Elements of control of voluntary movements. *Biofizika* 10: 135–141
- Bernstein NA (1967) *The co-ordination and regulation of movements*. Pergamon, Oxford
- Bouisset SM, Zattara M (1981) A sequence of postural movements precedes voluntary movement. *Neurosci Lett* 22:263–270
- Bouisset S, Zattara M (1990) Segmental movement as a perturbation to balance? Facts and concepts. In: Winters JM, Woo SL-Y (eds) *Multiple muscle systems. Biomechanics and movement organization*. Springer, Berlin Heidelberg New York, pp 498–506
- Burleigh AL, Horak FB, Malouin F (1994) Modification of postural responses and step initiation: evidence for goal-directed postural interactions. *J Neurophysiol* 72: 2892–2902
- Cordo PJ, Nashner LM (1982) Properties of postural adjustments associated with rapid arm movements. *J Neurophysiol* 47: 287–302
- Crenna P, Frigo C, Massion J, Pedotti A (1987) Forward and backward axial synergies in man. *Exp Brain Res* 65: 538–548
- Dick JPR, Rothwell JC, Berardelli A, Thompson PD, Gioux M, Benecke R, Day BL, Marsden CD (1986) Associated postural adjustments in Parkinson’s disease. *J Neurol Neurosurg Psychiatr* 49: 1378–1385
- Dietz V, Mauritz KH, Dichgans J (1980) Body oscillations in balancing due to segmental stretch reflex activity. *Exp Brain Res* 40: 89–95
- Dufosse M, Hugon M, Massion J (1985) Postural forearm changes induced by predictable in time or voluntary triggered unloading in man. *Exp Brain Res* 60: 330–334

- Friedli WG, Cohen L, Hallett M, Stanhope S, Simon SR (1984) Postural adjustments associated with rapid voluntary arm movements. I. Electromyographic data. *J Neurol Neurosurg Psychiatr* 51: 232-243
- Friedli WG, Hallett M, Simon S. R (1988) Postural adjustments associated with rapid voluntary arm movements. II. Biomechanical data. *J Neurol Neurosurg Psychiatr* 57: 611-622
- Horak FB, Esselman PE, Anderson ME, Lynch MK (1984) The effect of movement velocity, mass displaced and task certainty on associated postural adjustments made by normal and hemiplegic individuals. *J Neurophysiol* 62: 841-853
- Lacquaniti F, Maioli C (1989) The role of preparation in tuning anticipatory and reflex responses during catching. *J Neurosci* 9:149-159
- Latash ML, Aruin AS, Shapiro MB (1995a) The relation between posture and movement: a study of a simple synergy in a two-joint task. *Hum Mov Sci* 14: 79-110
- Latash ML, Aruin AS, Neyman I, Nicholas JJ (1995b) Anticipatory postural adjustments during self-inflicted and predictable perturbations in Parkinson's Disease. *J Neurol Neurosurg Psychiatr* 58: 326-334
- Massion J (1992) Movement, posture and equilibrium: interaction and coordination. *Prog Neurobiol* 38: 35-56
- Melvill-Jones G, Watt DGD (1971a) Observation on the control of stepping and hopping movements in man. *J Physiol (Lond)* 219: 709-727
- Melvill-Jones G, Watt DGD (1971b) Muscular control of landing from unexpected falls in man. *J Physiol (Lond)* 219: 729-737
- Nashner LM, Cordo PJ (1981) Relation of automatic postural responses and reaction-time voluntary movements of human leg muscles. *Exp Brain Res* 43, 395-405
- Nashner LM, Woollacott M (1979) The organization of rapid postural adjustments of standing humans: an experimental-conceptual model. In: Talbot RE, Humphrey DR (eds) *Posture and movement*. Raven, New York, pp 243-257
- Oddsson L, Thorstensson A (1986) Fast voluntary trunk flexion movements in standing: primary movements and associated postural adjustments. *Acta Physiol Scand* 128: 341-349
- Palmer E, Cafarelli E, Ashby P (1994) The processing of human ballistic movement explored by stimulation over the cortex. *J Physiol (Lond)* 481: 509-520
- Paulignan Y, Dufosse M, Hugon M, Massion J (1989) Acquisition of co-ordination between posture and movement in bimanual task. *Exp Brain Res* 77: 337-348
- Riach CL, Hayes KC, Lucy SD (1992) Changes in center of pressure of ground reaction forces prior to rapid arm movement in normal subjects and patients with cerebellar ataxia. *Clin Biomech* 7: 208-214
- Rossignol S (1975) Startle responses recorded in the leg of man. *Electroencephalogr Clin Neurophysiol* 39: 389-397
- Strauss H (1929) Des Zusammenschrecken. *J Psychol Neurol (Lpz)* 39: 111-231
- Struppler A, Gerilovsky L, Jakob C (1993) Self-generated rapid taps directed to the opposite forearm in man: anticipatory reduction in the muscle activity of the target arm. *Neurosci Lett* 159: 115-118
- Viallet F, Massion J, Massarino R, Khalil R (1992) Coordination between posture and movement in a bimanual load lifting task: putative role of a medial frontal region including the supplementary motor area. *Exp Brain Res* 88: 674-684